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Tree architecture in *Porterandia* (Rubiaceae)

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Summary. Plant architectural characteristics help distinguish *Porterandia* from its allies. The tree architectural model for *Porterandia* spp. studied is the model of Scarrone (according to the system of Hallé, Oldeman & Tomlinson), with the following defining features: an orthotropic, rhythmatically active terminal meristem which produces an indeterminate trunk, bearing tiers of branches, each branch complex orthotropic and sympodially branched as a result of terminal flowering. From field observations of a number of species and herbarium material generally, this was found to be representative of the genus as a whole. In *Porterandia*, the branch architecture is also distinctive, with the proximal parts of the branch system forming forks just below the inflorescences; an odd number of internodes between any two consecutive forks; and sympodial series of 2-internode segments at the distal portions of the branch system (i.e., at the crown periphery) with the inflorescences in "pseudo-lateral" position (pushed to one side of the developing sympodium).

Tree architecture defines the overall growth habit of a tree in terms of the growth behaviour of the stem and branches, in relation to the orientation of axes, whether these are determinate in relation to such phenomena as flowering, the growth of potential axillary meristems, and various factors affecting growth patterns, such as modularity and continuity in the development of parts (Hallé, Oldeman & Tomlinson 1978). Generally, detailed surveys of plant architecture within the Rubiaceae are still too few for this to be of major utility in taxonomy. This is understandable, in view of the need to make observations of young stages as well as changes during the development of the plant, in order to capture the various characteristics properly.

Although it was emphasized that architectural expression is a function of the species, it was also realized that taxa above the species sometimes displayed architectural unity (e.g., Myristicaceae and the genus *Diospyros*, Ebenaceae, are generally represented by Massart's model) (Hallé, Oldeman & Tomlinson 1978). Others (Fagerlind 1943, Petit 1964, Halle 1967, Tirvengadum & Sastre 1979, and Wong 1984) have pointed out interesting development of particular branching patterns, both within and between groups in the

Rubiaceae. Opportunity was taken to examine the growth architecture of *Porterandia* (Rubiaceae) during a taxonomic delimitation and revision of that genus (Zahid 2004), which is distinguished from taxa now placed within *Atractocarpus* (Puttock 1999) and *Bungarimba* (Wong 2004) through a suite of characters.

STUDY MATERIALS

Plant architecture was studied in the field for *Porterandia anisophylla* (at Bukit Engku Busu, Lumut, Perak; Pasoh Forest Reserve, Negeri Sembilan; Sungei Menyala Forest Reserve, Negeri Sembilan); *P. beamanii* (at the Tenompok Forest Reserve, Ranau, and the Rafflesia Forest Reserve, Tambunan, Sabah); *P. chanii* (at the Arboretum Forest Reserve, Sepilok, Sandakan, Sabah); *P. postarii* (at the Kuamas Forest Reserve, Telupid); *P. scortechinii* (at the Rimba Ilmu Botanic Garden, University of Malaya, Kuala Lumpur); and *Bungarimba ridsdalei* (at the Kinabalu National Park, Sabah).

Both young and adult plants were observed, in particular for the phyllotaxy (leaf arrangement) on vertical stem axes and branches, branching sequences and position of inflorescences. Complementary studies of branch structure and flowering and branching sequences were also made from herbarium specimens.

In the case of *Atractocarpus heterophyllus*, the architecture was interpreted from a collection at KLU (*Stone* 14914) and from pictures of its habit and branching by Daniel, Irène and Christian Létocart in the website of the Association ENDEMIA ("Endémia, Faune & Flore de Nouvelle Calédonie", http://www.endemia.nc/plante/ accessed on 31 October 2003).

PAST OBSERVATIONS ON *PORTERANDIA* BRANCHING

There are very few comments in the literature on the architecture of *Porterandia*. Tirvengadum & Sastre (1979) and Tirvengadum (1982) placed *Porterandia* together with *Aidia* in a category identified as their "Mode 8". Their diagrams of shoot sequences at the distal part of the branch system portrayed sympodial branch development as a basically linear progression with only one relay branch developing just below each inflorescence. The basically terminal inflorescence is pushed to one side during development of a relay branch axis from a leaf axil at the distal portion of the preceding axis.

Although Corner (1988) had also briefly commented on the unequal leaves of a pair in *P. anisophylla* and *P. scortechinii* (both recorded as *Randia*), he also did not provide any notes on tree structure. Corner (1988) pointed out as follows:

> "In the common little trees *R. anisophylla* and *R. scortechinii* the leaves of a pair on the horizontal twigs are generally very unequal, that on the upper side being

much smaller than that on the lower, and the flower-clusters always develop on the upper sides of the twigs, that is to say in the axil of what would be the small leaf of the pair; but this small leaf is then reduced to a vestige called a scale-leaf and the flower-cluster appears opposite a single big leaf." [pg. 646]

Corner (1988) appeared to have described flowering branches at the periphery of the crown, which differ from that found at more proximal parts of the branch system (see below).

Wong (1984) gave a brief survey of branching organization in a group of genera in Peninsular Malaysia previously confused with *Randia*, including *Porterandia* (represented by *P. anisophylla*). According to him, the first-order axis of each branch system (which originates from an axillary bud on the trunk) consistently has a proximal long internode followed by four shorter internodes before the terminal bud aborts and the first fork forms. At the first fork, the two branches are subequal in size but higher-order forks produce a smaller branch axis (which turns upwards and seldom reforks) and a larger branch axis which forks again. There are usually three or five (sometimes seven, nine or more) internodes between any two successive forks in the branch system (i.e., the number of internodes is always an odd number).

Wong (1984) did not identify the architectural growth model of *P. anisophylla* according to the system of Hallé, Oldeman & Tomlinson (1978). He also noted that the branching pattern of *Porterandia sessiliflora* (now *Bungarimba sessiliflora*) could not be precisely determined from the few specimens known to him.

BASIC ARCHITECTURAL ATTRIBUTES IN *PORTERANDIA*

The architecture of *Porterandia* trees can be analyzed according to the morphological principles given in Hallé, Oldeman & Tomlinson (1978). These authors provide information on 24 models they recognized for tropical trees. The several major elements for understanding the tree architecture of *Porterandia* (as represented by the species *P. anisophylla*, *P. beamanii*, *P. chanii*, *P. postarii* and *P. scortechinii*) are as follows:

i) Vertical / trunk system

The stem or trunk (Fig. 1) is a vertically growing, negatively geotropic axis that has a rhythmic or episodic growth, i.e., maximum height or length growth in particular intervals, interrupted by periods of slower growth. The slower growth phases of the vertical stem axis coincide with the development of branches, so that the branches along the stem appear grouped together in distinct tiers. The vertically growing stem axis is orthotropic in the sense of Hallé, Oldeman & Tomlinson (1978), i.e., it is negatively geotropic, has an essentially radial symmetry, decussate phyllotaxis, and branches three-dimensionally.

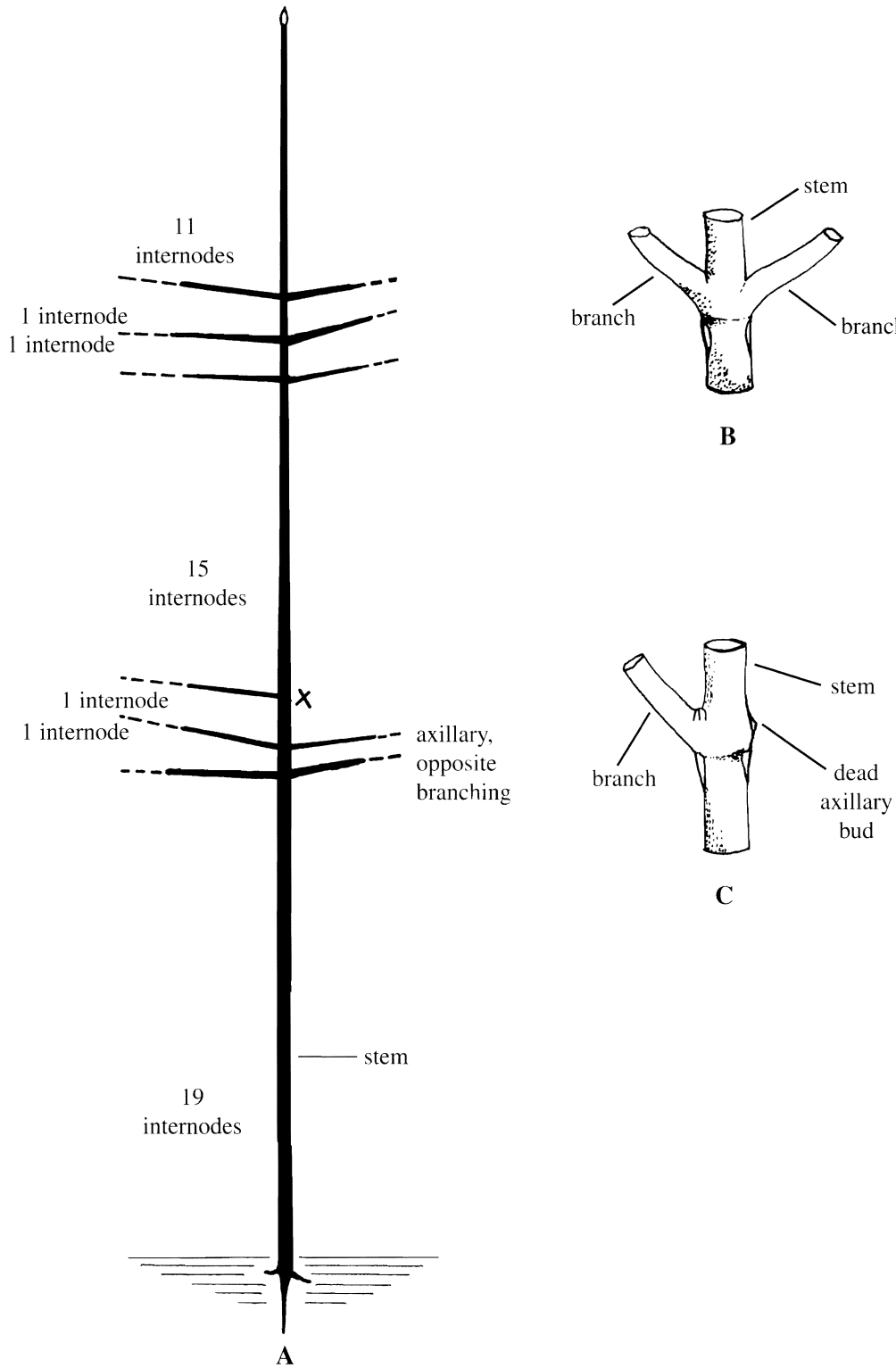

Fig. 1. Diagrammatic representation of episodic trunk growth and branch production in *Porterandia* (**A**); a section of the stem where typically a pair of branches have developed (**B**) and another where, exceptionally, one of a pair of axillary buds has failed to develop (**C**) are also shown. Failure of a bud or branch to develop is denoted by an 'x'.

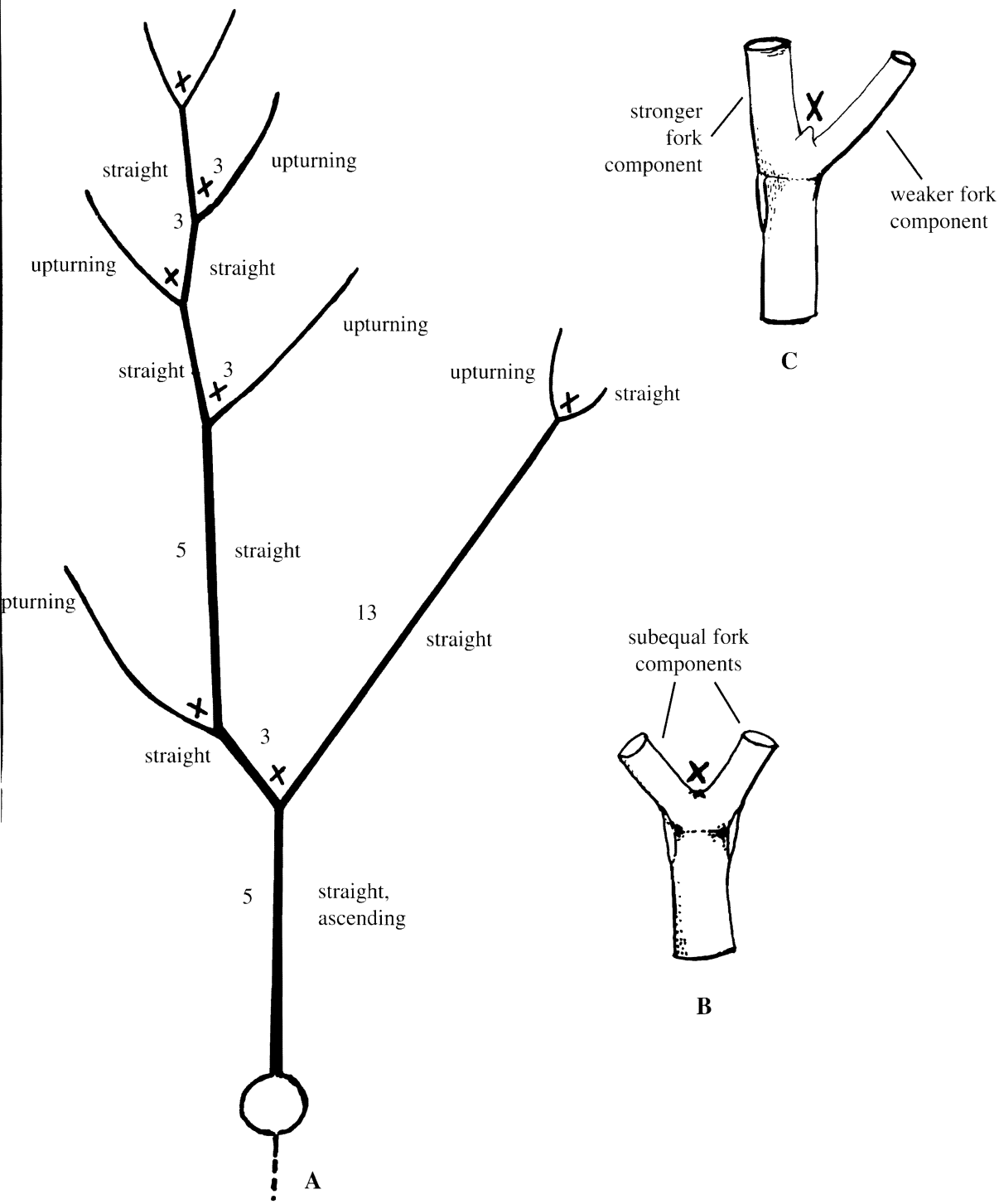

Fig. 2. Diagrammatic representation of a single branch system in plan view of *Porterandia scortechinii* (**A**) where the primary branch ceases growth and is succeeded by a pair of isotomous branches (detail in **B**) and subsequent forks are mostly anisotomous (detail in **C**), with the stronger member more-or-less growing straight and the weaker member upturning. Arrestment of terminal buds is denoted by 'x' and numbers indicate internodes between points of branching.

ii) Branch system

Branching is opposite and decussate on the orthotropic stem axis (Fig. 1), but occurs episodically. Each branch is sylleptic in its development in the sense of Hallé, Oldeman & Tomlinson (1978), i.e., it is produced through continuous growth of a lateral meristem after that forms, without an evident intervening period of rest. The branches are also orthotropic as defined above, as they bear oppositely and decussately arranged leaves and so are radially symmetrical, as well as negatively geotropic in orientation.

Each primary branch axis typically has a proximal long internode (about 3–4 times the length of internodes distal to it) and 2–4 short internodes, just before the terminal bud ceases growth and the first fork is formed by development of two axillary branches (Fig. 2). At the first fork, the two axillary branches are subequal in diameter. At subsequent forks (Fig. 2), one axis (or axillary branch) is larger and does not upturn but, instead, continues to extend the branch-system outwards; the other axis (or axillary branch) is smaller, upturns and seldom forks further (only very rarely do higher-order forks produce subequal branches) (Fig. 3). In between any two forks, as noted by Wong (1984), the number of internodes is an odd number, usually 3, 5, 7, or 9.

Fig. 3. Part of a branch system from a young *Porterandia beamanii* tree, showing a relay of branch segments of successively higher order.

This form of branching produces basically orthotropic units in succession, but the relay axes are not mainly in any linear progression because of the production of pairs of axillary branches at most points of branching. Therefore, this form of branching differs from what has been called "terminalian branching", which has been defined by Hallé, Oldeman & Tomlinson (1978) as a sympodial succession of branch axes of increasingly higher order, where the axis of the next higher order is always borne in a hypotonic position (i.e., on the lower side) on its parent axis where that axis begins to upturn. That mode of branching has been generally referred by Hallé, Oldeman & Tomlinson (1978) as modular branching with plagiotropy by apposition.

iii) Inflorescence development

The inflorescences are clearly terminal and are mostly formed at the end of a branch segment just at or following the production of a pair of axillary branches, as described above (Fig. 4). Conspicuous forks with inflorescence development in the angle between the two branches of a fork are very common in the branch system of the *Porterandia* tree.

However, at the periphery of the crown in a mature tree, and on the smaller upturned axes at some of the forks, only single branches develop below the point of flowering, and these continue a short growth of two internodes before they themselves flower. This makes the sympodial succession at the edges of the crown (of mature trees) and distal to some of the smaller upturned axes at forks resemble a sequence of 2-internode relay segments with lateral inflorescences (Fig. 5). Also, at such points where single rather than paired axillary branches are produced in association with flowering, the upper member of the leaf pair just below the inflorescence is often reduced to a scale-like structure.

Fig. 4. Inflorescence *of Porterandia scortechinii* developing in a clearly terminal position at the end of the main (primary) branch, with the concurrent development of a pair of subequal branches forming the first fork in the branch system.

Fig. 5. Distal portion of the branch system of *Porterandia chanii*, where the smaller branch members bear pseudolateral inflorescences and infructescences; these distal branches are in fact sympodia of 2-internode segments.

Using these aspects of structural development as criteria, the *Porterandia* tree architecture can be identified with the model of Scarrone as defined by Hallé, Oldeman & Tomlinson (1978). Scarrone's model has the following key features: an orthotropic, rhythmatically active terminal meristem which produces an indeterminate trunk, bearing tiers of branches, each branch complex orthotropic and sympodially branched as a result of terminal flowering.

This model has also been recognized for *Gardenia imperialis* (Rubiaceae) from tropical Africa as well as a number of species in other dicot families and, among monocots, several *Pandanus* spp. In their discussion, Hallé, Oldeman & Tomlinson (1978) remarked that a number of trees with Scarrone's model are typical of old pioneer or secondary forest. This is also true of many *Porterandia* species, which appear to be found in secondary forests or at least forest fringes.

PLANT ARCHITECTURE COMPARED FOR *PORTERANDIA* AND SOME ALLIES

The architecture is different in *Bungarimba*, of which *B. ridsdalei* has been specially studied for the present discussion on architecture. In *B. ridsdalei*, the primary branches also

arise as opposite and decussate pairs along the main orthotropic stem, which, in contrast, shows continuous growth. The branches along the main stem, therefore, are not grouped into distinct tiers, but are more-or-less regularly spaced. However, each primary branch is sympodially replaced after only two internodes, the apex either ceasing growth or producing an inflorescence that terminates further growth (Fig. 6). The general development of the branch system in *B. ridsdalei* is a rather horizontal relay of 2-internode segments that represent successively higher orders of branching. The morphologically terminal inflorescences are pushed to a lateral position (on the upper side of the branch system) by the development of the next branch segment, and so appear to be lateral and spaced at 2-internode intervals.

Also, in this species, every node immediately proximal to the inflorescence has the leaf on the upper side of the branch completely undeveloped, so that the inflorescence, after it is pushed to a lateral position by continuing sympodial branching, appears "leaf-opposed". Although it has not been possible to make detailed studies of the other species of *Bungarimba* in the field, branch sequences and inflorescence positions on herbarium specimens indicate that the architecture is the same as that in *B. ridsdalei*.

This kind of branch development in *Bungarimba* is an extreme form of modular branch construction and plagiotropy by apposition (although each branch module, which has

Fig. 6. Each branch portion in *Bungarimba ridsdalei* is made up of a sympodial series of 2-internode (or 2-node) segments, each segment with the proximal node bearing a normal leaf leaf pair and the distal node with only one leaf developed. Paired axillary branches can form at nodes with paired leaves.

basically opposite and decussate leaf arrangement, is orthotropic). Combined with its orthotropic, monopodial and continuously (not episodically) growing stem axis, this represents the architectural model of Petit as defined by Hallé, Oldeman & Tomlinson (1978).

Puttock (1999) has also commented that *Porterandia* may have close affinity with *Atractocarpus*. However, the type species of *Atractocarpus*, *A. heterophyllus*, has a different architecture. Its stem axis is orthotropic and continuous in growth (as evident from regularly spaced leaf pairs), hardly branched except for pairs of branches that bear a number of reduced leaf-pairs and a terminal inflorescence. The branches are orthotropic in orientation but typically not sympodially extended. Following Hallé, Oldeman & Tomlinson (1978), this architecture appears to be a rudimentary form of Stone's model which, however, typically has a sympodially extended and modular branch system. In addition, branch development in *A. heterophyllus* is extra-axillary, each branch emerging a little above the axil proper of the subtending leaf, whereas in *Porterandia* and "Bungarimba", the branches arise directly from the leaf axils. A comparison of the basic architectural features among *Porterandia*, *Bungarimba* and *Atractocarpus* is also provided in Wong (2004).

The architecture was the same for both *Aidia densiflora* and *A. racemosa*, here discussed because *Porterandia* was grouped with *Aidia* in Tirvengadum & Sastre's "Mode 8". In these species the branch system is a sympodial relay of 2-internode segments, the more proximal node of each segment with a pair of subequal leaves, and the more distal node with one leaf reduced to a scale (on the upper side of the branch); the inflorescence is terminal but pushed to the upper side of the branch, appearing leaf-opposed. The branches are thus plagiotropic by apposition and the overall architecture is similar to that of *Bungarimba*.

REITERATIVE GROWTH IN *PORTERANDIA*

The architectures as described conform to the basic growth form (or programme) of each species or group. Another perspective that was not possible to study in detail in the present work was what Hallé, Oldeman & Tomlinson (1978) called "reiteration", which they defined as the "development of shoots outside the normal expression of the architectural model of a tree, as a specialized environmental response". This specialized environmental response includes damage to plant axes.

On two occasions, such reiterative shoot development was observed for *Porterandia* in response to damage. In one instance, a *P. anisophylla* tree which had nearly all of its branches cut at their basal portion began to develop new axillary shoots just below the cut axillary branches. Only one additional axillary branch was observed below each cut branch, at the same node (Fig. 7). The growth orientation of this second axillary shoot was orthotropic. In the second instance, a young stem of *P. beamanii* was observed to begin developing a pair of axillary branches just below the damaged apex. Although both axillary

Fig. 7 (Left). A second set of axillary buds developing after the first set (that had developed into branches) were cut off from a young sapling of *Porterandia anisophylla.* **Fig. 8 (Right).** Both axillary branches from a node developing orthotropically, following damage to the original stem apex of a *Porterandia beamanii* sapling.

branches were morphologically orthotropic, one was more erect and began to replace the original stem (Fig. 8).

Inspection of fresh material showed that only one bud could be clearly seen in each leaf axil, so it would appear that a traumatic growth response to damage may sometimes produce additional axillary meristems. This, however, is not confirmed and requires many more observations of material of different ages and experimental damage.

LEAF REDUCTION, ANISOPHYLLY AND HETEROPHYLLY

In *Porterandia*, the anisophylly (unequal development of the two leaves of a pair) is observed for all the species. According to Robbrecht (1988), the occurrence of anisophylly is quite common among Rubiaceae taxa, especially in the Gardenieae. In *P. anisophylla* and *P. scortechinii*, Wong (1984) and Corner (1988) have noted that the leaf pairs which are

significantly oriented away from the horizontal plane have the leaf on the upper side of the branch reduced in size. This is true for all species in *Porterandia* that have been studied presently.

In *Bungarimba*, just below each inflorescence (which represents the apex of a single branch module), the upper leaf of a pair is totally undeveloped and absent, not merely smaller in size. In *A. heterophyllus*, the leaf pairs on the branches are of similar size, but these branch leaves are markedly smaller and often sessile or subsessile compared to the much larger stem leaves which are clearly petiolate. In other words, there are two leaf forms present together on the same plant, and this can be termed heterophylly rather than anisophylly, which might be more specifically used to refer to the existence of pairs of unequal-sized leaves.

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